Received: 13 March 2021 | Accepted: 14 October 2021

DOI: 10.1111/1365-2656.13615

Journal of Animal Ecology | BRITISH ECOLOGICAL SOCIETY

LONG TERM STUDY

Integrating advances in population and evolutionary ecology with conservation strategy through long-term studies of red-billed choughs

Jane M. Reid[1,2] | Eric Bignal[3] | Sue Bignal[3] | Davy I. McCracken[4] | Sarah R. Fenn[1] | Amanda E. Trask[5] | Pat Monaghan[6]

[1]School of Biological Sciences, Zoology Building, University of Aberdeen, Aberdeen, UK

[2]Centre for Biodiversity Dynamics, Institutt for Biologi, NTNU, Trondheim, Norway

[3]Scottish Chough Study Group, Kindrochaid, Bridgend, Isle of Islay, Argyll, UK

[4]Department of Integrated Land Management, Scotland's Rural College, Ayr, UK

[5]Institute of Zoology, Zoological Society of London, London, UK

[6]Institute of Biodiversity, Animal Health & Comparative Medicine, Graham Kerr Building, University of Glasgow, Glasgow, UK

Correspondence
Jane M. Reid
Email: jane.reid@abdn.ac.uk

Funding information
Royal Society for the Protection of Birds; Scottish Natural Heritage; University of Aberdeen; Jesus College, University of Cambridge; Natural Environment Research Council; University of Glasgow; Royal Society; Scotland's Rural College; Killam Trusts; Leverhulme Trust; Norwegian Research Council

Handling Editor: Anne Loison

Abstract

1. Conceptual and methodological advances in population and evolutionary ecology are often pursued with the ambition that they will help identify demographic, ecological and genetic constraints on population growth rate (λ), and ultimately facilitate evidence-based conservation. However, such advances are often decoupled from conservation practice, impeding translation of scientific understanding into effective conservation and of conservation-motivated research into wider conceptual understanding.
2. We summarise key outcomes from long-term studies of a red-billed chough *Pyrrhocorax pyrrhocorax* population of conservation concern, where we proactively aimed to achieve the dual and interacting objectives of advancing population and evolutionary ecology and advancing effective conservation.
3. Estimation of means, variances and covariances in key vital rates from individual-based demographic data identified temporal and spatial variation in subadult survival as key constraints on λ, and simultaneously provided new insights into how vital rates can vary as functions of demographic structure, natal conditions and parental life history.
4. Targeted analyses showed that first-year survival increased with prey abundance, implying that food limitation may constrain λ. First-year survival then decreased dramatically, threatening population viability and prompting emergency supplementary feeding interventions. Detailed evaluations suggested that the interventions successfully increased first-year survival in some years and additionally increased adult survival and successful reproduction, thereby feeding back to inform intervention refinements and understanding of complex ecological constraints on λ.
5. Genetic analyses revealed novel evidence of expression of a lethal recessive allele, and demonstrated how critically small effective population size can arise, thereby increasing inbreeding and loss of genetic variation. Population viability analyses

parameterised with all available demographic and genetic data showed how ecological and genetic constraints can interact to limit population viability, and identified ecological management as of primacy over genetic management to ensure short-term persistence of the focal population.

6. This case study demonstrates a full iteration through the sequence of primary science, evidence-based intervention, quantitative evaluation and feedback that is advocated in conservation science but still infrequently achieved. It thereby illustrates how pure science advances informed conservation actions to ensure the (short-term) stability of the target population, and how conservation-motivated analyses fed back to advance fundamental understanding of population processes.

KEYWORDS

adaptive management, applied ecology, conservation genetics, demography, evidence-based conservation, long-term study, population growth rate, population viability analysis

1 | INTRODUCTION

Numerous species are currently experiencing substantial declines or threats to global or local persistence, and are consequently subject to statutory or discretionary species-focussed conservation efforts on international and/or national scales (Hoffmann et al., 2010; Eaton et al., 2015; IPBES, 2019). Core principles of conservation science are that such efforts should be evidence-based and iterative, following sequences of (a) primary scientific investigation to identify mechanisms causing population declines or threats; (b) design and application of appropriate interventions; and (c) rigorous monitoring and evaluation that can feed back to inform subsequent intervention refinements and also advance wider understanding (Figure 1, Gillson et al., 2019). Yet, recent reviews suggest that such sequences of concept-driven primary science, intervention, (re-)evaluation and full feedback, and resulting joint application and facilitation of scientific advances, are still infrequently achieved (Cook et al., 2013; Gillson et al., 2019; Toomey et al., 2016; Walsh et al., 2014; Williams et al., 2020).

Any such failures cannot be attributed to a fundamental lack of scientific capability to understand and forecast population dynamics. Rather, recent decades have seen major conceptual and methodological developments in population and evolutionary ecology that facilitate the identification of demographic, ecological and genetic mechanisms causing population change, and allow the prediction of population outcomes given observed or postulated threats, forms of environmental change or policy-driven interventions. Not least, matrix models and advanced individual-based simulation methodologies allow projection of population growth rate (λ) and persistence given complex age and/or stage structure, including estimation of stochastic growth rates (λ_s) in temporally and/or spatially varying environments (e.g. Bocedi et al., 2014; Boyce et al., 2006; Caswell, 2001; Lacy & Pollak, 2017). Given estimates of mean vital rates, comprising age- and/or stage-structured reproduction and survival probabilities,

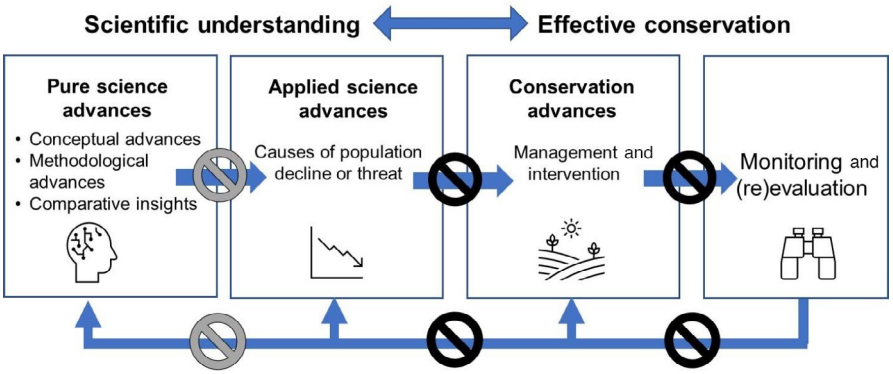

FIGURE 1 Summary of ambitions for integrating advances in fundamental scientific understanding and effective conservation. Pure science advances are applied to identify causes of population decline or threat. Interventions are designed, implemented, monitored and evaluated, with results fed back to advance both pure and applied understanding. Gaps can potentially arise in translating applied science into interventions and re-evaluations (⃠) and in translating pure into applied science and vice versa (⃠). The long-term chough study aimed to proactively integrate pure and applied science and conservation interventions and foster two-way feedbacks, and thereby minimise all these potential gaps

matrix models also facilitate prospective elasticity analyses to identify rates in which small changes would have greatest impact on λ (Caswell, 2000, 2001), including 'integrated elasticities' that incorporate vital rate covariation (van Tienderen, 1995). Estimation of among-year variation in vital rates also allows retrospective analyses that identify which rates caused observed variation in λ, thereby identifying actual demographic causes of population change (i.e. 'life table response experiments', Caswell, 2000; Wisdom et al., 2000). Meanwhile, theoretical advances at the interface of population and evolutionary ecology show how age- and/or stage-specific reproductive value can be coupled with demographic variance to estimate effective population size (N_e), and hence evaluate the rates of genetic drift and the accumulation of inbreeding (Engen et al., 2005, 2007). These objectives reflect growing evidence that genetic constraints associated with small population size, particularly inbreeding and resulting expression of inbreeding depression, can substantially limit λ (Bozzuto et al., 2019; Frankham et al., 2014). Consequently, the need to consider genetic constraints on population persistence alongside ecological constraints is now strongly advocated (Allendorf et al., 2021; Frankham et al., 2017; Haig et al., 2016).

Such conceptual developments in population and evolutionary ecology have occurred alongside major statistical and empirical developments which allow theory to be tested and applied in wild populations. Specifically, advanced capture–mark–recapture methods can reduce bias in estimation of vital rates and life-history variation from incomplete data where, as is almost inevitable in wild population studies, not all present individuals are always observed (Gimenez et al., 2008; Nichols & Kendall, 1995; White & Burnham, 1999). Meanwhile, field studies are accumulating sufficient years of individual-based data to allow the estimation of vital rate means, variances and covariances, and associations with underlying environmental variation. Comparative demography databases have been compiled, and there are sufficient estimates of key parameters, such as the magnitude of inbreeding depression, to allow broad comparative insights into likely constraints on populations for which direct data are sparse or even completely lacking (e.g. Frankham et al., 2014; Frankham et al., 2017; Salguero-Gómez, 2016).

Such theoretical, statistical and empirical advances are often initially pursued within 'pure' science programmes, where the primary ambition is conceptual advance rather than direct application. Yet, even pure science programmes commonly invoke explicit or implicit justifications that resulting insights will ultimately facilitate population management and/or conservation. However, in practice, there is a widely acknowledged research implementation 'gap' or 'space', such that new knowledge is not rapidly translated into conservation interventions for threatened populations (Figure 1; Cook & Sgrò, 2017; Dubois et al., 2020; Jarvis et al., 2020; Toomey et al., 2016). Such gaps are commonly emphasised regarding translation of directly relevant applied research into conservation action (Figure 1; Arlettaz et al., 2010; Taylor et al., 2017; Walsh et al., 2014). But, there can be further gaps, whereby conceptual and methodological advances achieved at the cutting edges of pure population and evolutionary ecology are not utilised in applied research (Figure 1). Furthermore, while it is frequently emphasised that conservation interventions should be monitored and evaluated to refine actions, the opportunity for research motivated by application and evaluation to feed right back to advance general conceptual understanding (Figure 1) is less frequently highlighted or exploited (Cook et al., 2013). Pure and applied science disciplines then do not fully embrace each other, to the likely detriment of both and to the ultimate conservation objectives.

Such divisions have been shown or suggested to persist because research in population and evolutionary ecology versus applied conservation is often undertaken by separate groups and organisations with differing objectives, priorities, capabilities and value systems (Arlettaz et al., 2010; Cook et al., 2013; Gillson et al., 2019; Jarvis et al., 2020; Roux et al., 2019; Toomey et al., 2016; Walsh et al., 2014). This leads to dysfunctional communication, arising partly because concept-led scientific publications by academic researchers are not always accessible, intelligible or apparently relevant to applied scientists and practitioners (Fabian et al., 2019; Taylor et al., 2017; Walsh et al., 2014). These divisions can be further exacerbated because pure science advances are often achieved using populations or species that are not themselves of current conservation concern but where multi-year observational and/or experimental data can be relatively readily collected. Meanwhile, key data required for advanced demographic and/or genetic analyses often cannot be readily or adequately collected in populations for which conservation action is urgently required, and/or primary publications focus on general concepts and follow editorial policies to downplay system-specific inferences that could facilitate management.

These challenges raise questions regarding the degree to which rapid applications of advances in population and evolutionary ecology are achievable within current professional structures and constraints and how such integration can be improved (Cook et al., 2013; Cook & Sgrò, 2017; Enquist et al., 2017; Jarvis et al., 2020; Taylor et al., 2017; Toomey et al., 2016), or else to what degree ultimate conservation application is actually a valid justification for investment in pure science programmes. Reflective case studies that summarise and evaluate efforts at pure–applied integration (Figure 1), and identify achievements and failures, can then provide useful context and insights to establish and encourage best practice (Arlettaz et al., 2010; Gillson et al., 2019; Williams et al., 2020).

Accordingly, we review key outcomes from long-term individual-based research on a red-billed chough (*Pyrrhocorax pyrrhocorax*, hereafter 'chough') population of conservation concern, where we explicitly aimed to achieve the joint, interacting, goals of advancing fundamental scientific understanding and advancing effective conservation (Figure 1). Specifically, we summarise five research phases that utilised conceptual and methodological advances at the forefronts of population and evolutionary ecology to identify constraints on population size and persistence, and to inform and evaluate resulting conservation interventions (Figure 2). We thereby highlight how pure science advances contributed to conservation actions and evaluations, and also highlight how research motivated primarily by conservation application fed back to advance conceptual

understanding. We summarise the process of pure–applied translation, and highlight remaining challenges in achieving desired conservation outcomes.

2 | FIELD STUDY AND CONSERVATION CONTEXT

Choughs are corvids that are closely associated with low-intensity pastoral agricultural habitats. They were formerly widespread across the British Isles, but decreased substantially in population size and distribution over the last two centuries (Bignal et al., 1997; Hayhow et al., 2018). Choughs are consequently listed on Annex 1 of the EU Wild Birds Directive and Schedule 1 of the UK Wildlife & Countryside Act, triggering statutory conservation obligations. In particular, NatureScot, the delegated Scottish Government agency, is responsible for safeguarding Scotland's chough population, which is now restricted to the inner Hebridean islands of Islay and Colonsay (Figure 2, Hayhow et al., 2018). Since choughs are classed as vulnerable and the UK subspecies is amber-listed (Eaton et al., 2015; Stanbury et al., 2017), chough conservation has also been a focus for the Royal Society for the Protection of Birds (RSPB, a non-governmental organisation), including reserve acquisition and management.

On Islay, chough research has been ongoing since 1981, including a licensed programme of nest monitoring, individual colour-ringing and resightings run by Scottish Chough Study Group (SCSG, Appendix S2). In brief, adult pairs occupy large territories where they breed once each year during April–June. Nests are traditionally in caves in sea cliffs, but increasingly in farm buildings and custom-built field shelters (Figure 3; Bignal et al., 1997; Hayhow et al., 2018). The locations of most potential nest sites are consequently known, facilitating demographic monitoring.

Each year, a sample of accessible cave and building sites is visited to record breeding success, and chicks are colour-ringed to allow subsequent individual identification (Figure 3). Nests are usually only visited once per year to minimise disturbance, coinciding with expected chick ringing age (approximately 3–4 weeks post-hatch), but second visits are made if chicks are initially too small. Adults are not caught, again to minimise disturbance. However, survival of colour-ringed fledglings means that ≥60% of adults are now colour-ringed. Adults at accessible and inaccessible nest sites are checked for colour-rings by remote observation (rings readable at ≤300 m through a telescope, Figure 3). Year-round resighting effort in foraging and roosting areas also provides numerous observations of surviving subadults.

The main demographic monitoring dataset now comprises >2,050 individuals ringed during 1983–2019, with >35,000 subsequent resightings and >1,400 observations of breeding success, allowing estimation of key vital rates that determine λ. Since the population is currently effectively closed with no recent detected immigration or emigration, survival probabilities can be estimated with little or no bias due to emigration, and population dynamics are determined by local demography rather than movements. Yet, while the insular system facilitates demographic analyses, it also fosters inbreeding.

Early research focussed on understanding social roosting behaviour (Still et al., 1987) alongside species ecology and life history (e.g. Bignal et al., 1997; Laiolo et al., 1998; McCracken & Foster, 1994; McCracken et al., 1992). Meanwhile, the number of breeding pairs on Islay decreased from 78 in 1986 to 47 in 1998 (Figure 2), increasing the urgency to implement evidence-based conservation to reverse the population decline. Accordingly, in 2001, efforts commenced to couple the accumulating demographic data with recent conceptual and statistical advances in population and evolutionary ecology to inform conservation strategy (Figures 1 and 2).

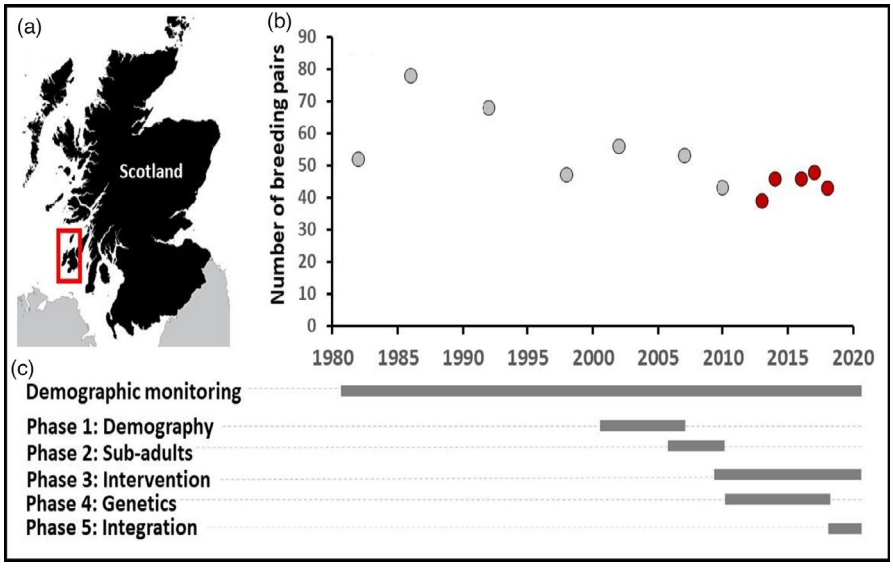

FIGURE 2 (a) Locations of Scotland's remaining chough populations on Islay and Colonsay (red box). (b) Chough population size (number of breeding pairs) on Islay in full census years during 1982–2018. Red points denote censuses during a supplementary feeding intervention. (c) Timelines of demographic monitoring and five primary research phases: (1) Population demography and dynamics, (2) Ecology of subadult survival, (3) Emergency intervention and evaluation, (4) Genetic constraints and (5) Integration of ecological and genetic threats

FIGURE 3 Examples of chough nest sites in (a) natural sea cave and (b) field shelter built in an inland habitat area, of colour-ringed (c) adult and (d) fledgling, and of (e) choughs attending supplementary feeding and (f) a blind chick. Photos: (a, b, d, e and f) Scottish Chough Study Group, (c) Gordon Yates

3 | RESEARCH PHASES

3.1 | Phase one: Population demography and dynamics

In general, first major steps towards understanding and managing population dynamics are to quantify temporal and spatial (co)variation in vital rates, and identify underlying drivers and impacts on λ. Accordingly, we used demographic data from 1983 to 2000 to show that among-year variation in mean breeding success (fledglings/breeding attempt) was correlated with variation in weather. Specifically, choughs bred more successfully in springs following warmer previous summers and relatively dry late winters, perhaps reflecting lagged weather effects on invertebrate prey (Reid et al., 2003a). Capture–mark–recapture analyses of ring-resighting data showed that first-year survival probability (i.e. survival from ringing to approximately 1 year old) also varied substantially among years (Figure 4), and was strongly positively correlated with population mean breeding success in each cohort's natal year (Reid et al., 2003a). Furthermore, the probability that an individual would survive to recruit to breed (typically age 3 years), adult life span and total lifetime number of offspring fledged were all also positively correlated with mean population breeding success in the natal year, and hence with underlying environmental conditions (Reid et al., 2003a).

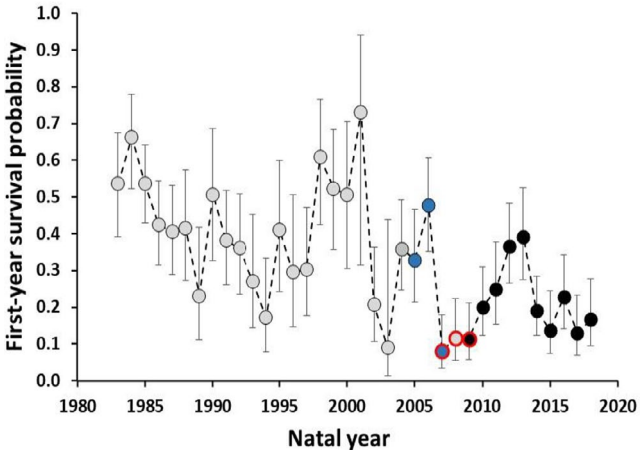

FIGURE 4 Estimated first-year survival probabilities (with 95% confidence intervals). Grey fill denotes years of baseline demographic monitoring. Blue fill denotes years of intensive monitoring of subadults. Red outline denotes three successive years of very low survival. Black fill denotes years of supplementary feeding

These analyses, which utilised recent advances in capture–mark–recapture methodologies, provided evidence of strong and long-lasting cohort effects, which had not then been widely demonstrated in wild populations (Lindström, 1999). They also implied strong local

environmental influences on overall annual productivity, indicating that long-term legacies of beneficial early-life environmental conditions might substantially influence individual fitness and hence population growth.

Further capture–mark–recapture analyses showed that adult survival probability (i.e. survival through each year from age 2) was high and varied relatively little among years, while second-year survival probability (i.e. survival from age 1 to 2) was intermediate (Reid et al., 2003a, 2004). Resulting estimates of means, variances and covariances in stage-specific survival and reproductive success allowed parameterisation of matrix models. Here, initial analyses showed that population dynamics were well captured by a four-stage model, comprising first-year, second-year, third-year and adult classes (Reid et al., 2004). Indeed, the modelled population trajectory matched population census data remarkably well, implying that available demographic data allowed unbiased estimation of all key vital rates (Reid et al., 2004). The four-stage model performed well despite evidence that breeding success varied with age within the adult class, including apparent senescence (Reid et al., 2003b, 2004). Since few individuals survived to ages at which vital rates decreased, any senescence scarcely affected annual population mean rates or resulting estimates of λ (Reid et al., 2004). Yet, while they proved non-essential for projecting short-term population dynamics, underlying analyses of age-specific variation provided new conceptual understanding of how interactions among age, reproductive success and longevity, and resulting selective disappearance, can generate actual and apparent senescence through joint cross-sectional (among-individual) and longitudinal (within-individual) variation in age-specific reproductive performance (Reid et al., 2003b).

Asymptotic λ, simply estimated as the dominant eigenvalue of the mean projection matrix, was approximately 1, projecting stable population size. However, the approximate stochastic growth rate was $\lambda_s \approx 0.97$, indicating gradual population decline (Reid et al., 2004). This estimate concurred with the observed decrease in population size (Figure 2) and illustrates the common impact of among-year variation in vital rates in reducing λ (e.g. Boyce et al., 2006; Hilde et al., 2020).

As is typical for reduced dimension matrix models parameterised for species with relatively slow life histories, prospective analyses indicated that λ was more elastic (i.e. proportionally sensitive) to adult survival probability than to subadult (i.e. first-year or second-year) survival probabilities, or to breeding success (Reid et al., 2004). This was also true given integrated elasticities that accounted for covariances among vital rates across years, but the summed elasticity across the subadult classes was relatively high (Reid et al., 2004). Furthermore, because subadult survival probabilities varied more among years than adult survival probabilities, retrospective 'life table response experiments' showed that first-year, second-year and adult survival contributed similar to variation in λ, with a major overall contribution from the combined subadult class (Reid et al., 2004). These analyses identified that variation in subadult survival could play, and had played, a major role in shaping population dynamics. This conclusion broadly concurs with observations from other species with relatively slow life histories, where juvenile survival also varies substantially among years (e.g. Gaillard et al., 1998). But, still relatively few studies have explicitly quantified vital rate covariation or resulting integrated elasticities, or hence estimated total effects of (co)variation involving juvenile survival on population dynamics (Coulson et al., 2005; Hilde et al., 2020).

Fully understanding links among environmental variation, demography and population dynamics requires considering spatial as well as temporal variation in vital rates. Although the total chough suitable area on Islay is relatively small (<200 km^2), it encompasses diverse grassland habitats that are exposed to open Atlantic coasts or more sheltered (Figure 3), with different underlying geologies, ecologies and pastoral agricultural regimes. We showed that first-year survival probability varied spatially, such that choughs hatched in some areas of Islay were consistently more likely to survive to age 1 year than choughs hatched in other areas (Reid et al., 2006). This was true even though choughs fledging in all areas typically congregate in communal foraging and roosting areas after fledging, and are no longer associated with their natal territory (Bignal et al., 1997; Still et al., 1987). Our analyses also revealed notably long-lasting associations between an individual's natal area and its adult survival probability. Unexpectedly, natal area explained more variation in annual adult survival than current breeding area (Reid et al., 2006). These analyses further affirmed the long-lasting impacts of natal conditions in driving variation in survival across all life stages, and hence in λ. They identified key 'source' areas within Islay that were apparently responsible for maintaining population viability, and which differed somewhat from previous conceptions of core chough habitat.

The general concept of 'silver-spoon effects', meaning long-term effects of good early-life conditions, is now well established in ecology and evolutionary biology, including recognition that ultimate effects can differ among ages and subsequent environmental conditions (e.g. Cooper & Kruuk, 2018; Pigeon et al., 2019). Yet, such effects are still predominantly considered in relation to temporal (often among-cohort) environmental variation rather than spatial variation (but see van de Pol et al., 2006). Consequently, the possibility that source areas that drive population growth may be missed or erroneously attributed by measuring survival across current inhabitants is still infrequently considered.

3.2 | Phase two: Ecology of subadult survival

Overall, the demonstration that subadult survival varied temporally and spatially in association with environmental conditions suggested that stochastic population growth rate λ_s, and hence population size, could potentially be effectively increased by increasing mean subadult survival and/or reducing frequencies or degrees of poor survival years or locations. This diagnosis prompted new focus on identifying constraints, and potential conservation interventions, that could target subadults. While basic subadult chough ecology and communal roosting behaviour were already understood (Bignal et al., 1997; Still et al., 1987), we lacked sufficient information on

early-life movements, habitat use and ecology to inform targeted conservation interventions.

Accordingly, we undertook intensive fieldwork to track two chough cohorts (2006–2007) from fledging through their first year and identify key foraging locations and habitat types (Reid et al., 2009). Meanwhile, we used the accumulating demographic data (1983–2007) to test specific hypotheses regarding the ecological basis of temporal (among-year) and spatial (among-territory) variation in first-year survival probability. We showed that temporal variation was strongly positively correlated with tipulid larvae abundance (Figure 5, Reid et al., 2008). Tipulids are one major winter food for choughs, and abundance was monitored annually across southwest Scotland (including some sampling sites on Islay) to inform agricultural pest management. Overall, first-year survival probability was higher when choughs fledged following and before winters with high tipulid abundance, and also following relatively warm summers and dry springs. Together, these variables explained up to ~80% of estimated among-year process variation in first-year survival probability (Reid et al., 2008). Our analyses were consequently successful in identifying specific components of early-life environmental variation that could drive first-year survival; such effects are often postulated across diverse bird species but still infrequently rigorously quantified (Maness & Anderson, 2013).

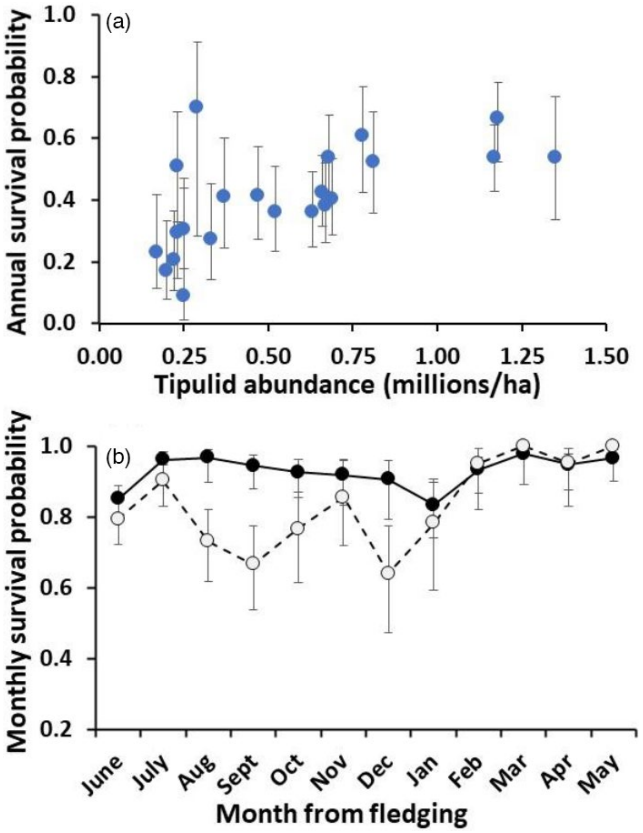

FIGURE 5 (a) Relationship between first-year chough survival probability and tipulid abundance (millions/hectare) in the winter before fledging. (b) Monthly survival probabilities of juvenile choughs fledged in low and high survival cohorts (open and filled symbols respectively)

In contrast, attempts to explain among-territory variation in first-year chough survival probability, and thereby identify determinants of 'source' areas, were less successful. This was partly because data on postulated drivers (e.g. prey abundance and various forms of land management) were not available on sufficiently small spatial scales (Reid et al., 2008). Nevertheless, the analyses of temporal variation strongly indicated that years of low first-year survival partly reflect early-life food limitation, which could underlie the previously documented long-term cohort effects and impacts on λ (Reid et al., 2003a; Reid et al., 2004, 2008). The attempts to understand variation in first-year survival for applied purposes also advanced general conceptual understanding by revealing that parents with long life spans systematically produced offspring with low survival probabilities, thereby highlighting how offspring survival can vary as a function of parental life-history strategy (Reid et al., 2010).

At this stage, attempts were made to integrate new knowledge of ecological constraints on key vital rates (Reid et al., 2006, 2008, 2009), into conservation action. In 2006, NatureScot added choughs as a qualifying interest for Islay's Gruinart Flats Special Protection Area (SPA), which was already designated due to its internationally important wintering goose populations (Appendix S1). This SPA encompassed key subadult chough foraging areas (Reid et al., 2009), and breeding territories that produced fledglings which survived relatively well (Reid et al., 2006, 2008). However, the designation process revealed that high survival probability is not listed as a qualifying criterion in SPA legislation (Appendix S1). There is consequently no legal basis to designate SPAs covering areas that are known to drive population growth by facilitating high survival for any species. This contrasts with clear scientific understanding that λ can be highly sensitive to variation in survival, representing a disconnect between conceptual understanding and conservation legislation. Choughs were consequently added to the Gruinart Flats SPA designation because the focal area qualified by holding >1% of the total UK population (Appendix S1); the desired science-informed designation was therefore achieved through valid but tangential criteria. But, further areas that supported high first-year survival did not contain existing SPAs. Legislative, political and economic constraints were viewed as being too strong to support completely new SPAs, and no such designations were attempted.

Management options designed to benefit choughs were also incorporated into the Scottish Rural Development Programme (SRDP) agri-environment scheme (Appendix S1). Since detailed agricultural management data were not available to directly relate to chough demography, SRDP options were designed based on expert knowledge, including from SCSG. They incentivised agricultural practices designed to benefit breeding and subadult choughs, for example, by adjusting year-round grassland management regimes. There was extensive uptake by farmers in key areas of Islay. However, initial option design and uptake were impeded by constraints on financial incentives due to restrictive definitions of relatively high-value 'in-bye' grassland that did not apply to less favoured agricultural areas

of high nature value, and potential conflicts with other conservation-focussed options. This included existing grassland management designed to benefit corncrake *Crex crex*, which has been highlighted as a successful yet necessarily ongoing agri-environment intervention (Green, 2020; Wotton et al., 2015).

3.3 | Phase three: Emergency intervention and evaluation

While conservation science should ideally pre-emptively prevent catastrophic demographic changes that induce rapid population decline, researchers and practitioners should be alert to unexpected challenges. During efforts to implement appropriate agri-environment options within the SRDP, ongoing chough demographic monitoring revealed a severe decrease in first-year survival probability on Islay, down to approximately 0.1 for cohorts fledged in 2007–2009 (Figure 4) compared to a previous mean of 0.42. Reparameterisation of matrix models with such low values projected rapid population decline ($\lambda = 0.87$, Reid et al., 2004, 2011). Urgent conservation action to maintain sufficiently high subadult survival to ensure population persistence was therefore required. This in turn required identification of the timing and causes of increased early-life mortality.

This objective was achieved through further analyses of long-term colour-ring-resighting data. Comparisons of monthly survival probabilities for three recent low-survival cohorts (2007–2009) versus earlier cohorts with higher first-year survival (1984–1986, 2005–2006) revealed a new period of low survival through late summer and autumn for the recent cohorts (Figure 5, Reid et al., 2011). Further observations showed that subadult choughs were feeding in atypical areas (e.g. on beaches), and post-mortem examinations of individuals found dead showed emaciation. This further supported previous inferences (Reid et al., 2008) that food shortage was constraining first-year survival and hence λ.

These analyses led directly to a targeted emergency supplementary feeding intervention designed to increase post-fledging survival, particularly through late summer and autumn. Starting fully from 2010, restricted quantities of supplementary food were provided almost daily during July–April through each biological year (i.e. excluding the main April–June breeding season) at or near known subadult roosting or foraging sites, thereby minimising disruption to natural foraging ecology (Trask et al., 2020). Feeding was designed as a top-up, providing only approximately 15% of a chough's estimated daily energy expenditure (Bignal & Bignal, 2011). High-frequency observations of colour-ringed individuals at feeding sites, currently totalling >95,000 resightings, showed that both subadults and adults regularly attended (Figure 3). We therefore evaluated whether the supplementary feeding intervention was effective in increasing first-year survival (as planned), and/or had collateral (i.e. unplanned) effects on adult survival or breeding success. Since the intervention was implemented as an emergency conservation action, not as randomised, replicated, controlled experiments, we utilised all available data from the intensive year-round demographic monitoring during the intervention period, and from previous baseline monitoring, to draw the best possible inferences.

We used multi-state capture–mark–recapture models to simultaneously estimate the proportion of juvenile choughs that attended supplementary feeding sites during defined occasions through the months following fledging, and to estimate survival probability conditional on attendance. These analyses showed that substantial proportions of surviving juveniles (≥70%) typically attended, and that survival probabilities were higher in individuals that attended than those that did not. However, such effects were not evident for all occasions within years, or evident at all in two of eight intervention years when overall annual survival probability was relatively high (Fenn et al., 2021). This implies that intervention efficacy varied with underlying ecological circumstances. Nevertheless, scaling estimated effects up to the population level suggested that the intervention greatly reduced the decrease in population size that was otherwise projected, solely through effects on the target vital rate of first-year survival (Fenn et al., 2021). These positive effects provide further quasi-experimental support for the original inference that food limitation constrained juvenile survival and hence λ. More generally, they show how intervention effects can vary temporally both within and among years, and hence have complex population-level effects (Fenn et al., 2021).

While the need to evaluate intervention effects on target individuals is frequently emphasised, evaluations of collateral effects on non-target conspecifics are less commonly attempted or achieved, even though such effects could have substantial positive or negative effects on λ. Accordingly, we estimated the effects of supplementary feeding on adult choughs that consistently did or did not attend feeding sites through each non-breeding season. Since adult attendance was structured with respect to territory location, resightings through the 8-year intervention period were coupled with resightings from pre-intervention years to control for spatial environmental variation using before-after-control-intervention (BACI) analyses. Such analyses are widely advocated, especially where formal experiments are impossible, but still relatively rarely implemented (Christie et al., 2019). We showed that adults that attended feeding sites had higher annual survival probabilities, and higher probabilities of successful reproduction, than adults occupying the same territories in previous years, while adults currently occupying other territories did not (Fenn et al., 2020). The estimated increases in adult survival were substantial and, alongside estimated moderate increases in nest success, were almost sufficient to maintain λ close to one and hence maintain population stability (Fenn et al., 2020).

These effects on adults were unanticipated in that previous demographic analyses in the chough system had not revealed substantial among-year variation in adult survival probability after accounting for sampling variance, or any recent decrease, and hence had not generated any inference that adults were substantially food limited. Indeed, it is widely expected that adult survival should be buffered from environmental variation in species with relatively slow life histories (Hilde et al., 2020). Our analyses, therefore,

highlight how implementation and full evaluation of conservation interventions, including collateral as well as planned impacts, can feed back to update the understanding of underlying constraints on vital rates and λ (Figure 1). They should also provide some optimism, since provision of even relatively little supplementary food increased projected population viability. NatureScot consequently extended the supplementary feeding programme to 2022, to allow more time to plan habitat management measures that could provide sustainable natural food (Appendix S1).

Together, research phases 1–3 represent a full iteration through the desired process of primary science, intervention, evaluation and feedback to allow refinement of both intervention and fundamental understanding, as advocated but still infrequently achieved in conservation science (Figure 1; Gillson et al., 2019; Williams et al., 2020).

3.4 | Phase four: Genetic constraints

The emergence of conservation genetics as a major discipline is partly founded on increasing evidence that inbreeding depression can be severe and constrain the viability of small populations (Allendorf et al., 2021; Bozzuto et al., 2019; Frankham et al., 2017; Haig et al., 2016). Accordingly, there was increasing concern that genetic constraints might proximately limit λ in Scottish choughs, alongside ecological constraints. Indeed, population genetic analyses based on bespoke microsatellite markers showed strong genetic structure across Scottish and other British and western European chough populations, with particularly low marker diversity in Scotland (Wenzel et al., 2011, 2012). These genetic data support inferences from colour-ring resightings that between-population dispersal and resulting gene flow is currently very infrequent or non-existent, even between the adjacent Islay and Colonsay populations (now 25 years since the last known effective dispersal over only ~10 km of sea). Inbreeding must consequently be accumulating.

Indeed, observations of blindness in chough chicks provided compelling evidence of negative genetic effects. Individuals' eyes failed to develop properly, with severe corneal opacity analogous to the human genetic disease 'Peters' anomaly' (Figure 3). Blind chicks could survive to fledging, but inevitably died subsequently. Detailed analyses showed that blindness afflicted exactly 25% of chicks in affected families on average (i.e. families where ≥1 blind chick was observed across years, Trask et al., 2016). This matches the frequency expected if blindness is caused by a single locus recessive allele with Mendelian inheritance, expressed in a homozygous state. While expression of lethal recessive alleles in inbred populations might be expected, in fact there are still very few documented instances in wild populations (Trask et al., 2016). Blindness in Scottish choughs is consequently a textbook example of manifestation of lethal genetic disease in a small wild population of conservation concern (Allendorf et al., 2021).

Overall, blindness affected only ~3% of chicks inspected on Islay during 1988–2014. Nevertheless, this frequency implies that the putative underlying recessive allele occurs at a non-trivial frequency of approximately 10%. There are intriguing indications that this may partly reflect overdominance resulting in increased reproductive success of heterozygous carriers; brood sizes in affected families were relatively large, almost compensating for mortality of blind chicks (Trask et al., 2016). Microsatellite-based estimates of relatedness showed that affected families were not more closely related to each other than to unaffected families, implying that the blindness allele is widely distributed in the contemporary population rather than restricted to a single lineage, and hence may have arisen numerous generations ago (Trask et al., 2016). It would therefore be difficult or impossible to eradicate, for example, through selective euthanasia, even if diagnostic genetic markers to identify heterozygous carriers were developed. Since phenotypic expression of blindness is infrequent (requiring homozygosity), it is not currently a major constraint on population-wide first-year survival probability or hence on λ. However, it could be symptomatic of a bigger problem of inbreeding and associated inbreeding depression in survival and/or reproductive success expressed across the population.

To consider this, it is informative to estimate effective population size (N_e), which dictates the rates at which inbreeding will accumulate and genetic variation lost through drift. N_e is defined as the size of an idealised Wright–Fisher population that would experience the same rate of genetic drift as an observed focal population. N_e is commonly substantially smaller than a population's observed census size N_c (i.e. small N_e/N_c ratio) because key Wright–Fisher assumptions of random within-generation mating with a Poisson distribution of effective reproductive success in both sexes are typically violated. However, it remains difficult to quantify N_e, and hence N_e/N_c, in wild populations (Frankham et al., 2014). Recent methods to estimate N_e from individual-based demographic data utilise matrix model estimates of age- or stage-specific reproductive value and concepts of demographic stochasticity and resulting variance, but have rarely been implemented (Engen et al., 2005, 2007). Accordingly, we used the long-term demographic data to apply these methods to estimate N_e for Islay's chough population, giving values of $N_e/N_c \approx 0.2$ and $N_e \approx 30$ (Trask et al., 2017). This value of N_e also broadly concurred with estimates calculated from advanced analyses of microsatellite marker variation (Trask et al., 2017). A value of $N_e \approx 30$ is critically small, smaller than any proposed rule-of-thumb minimum for short-term population viability (Frankham et al., 2014). It implies that inbreeding will accumulate relatively quickly in the continued absence of gene flow.

The fact that N_e is small could arguably have been directly and simply inferred from the fact that N_c is small (Figure 2). However, the explicit estimate of $N_e \approx 30$, coupled with blindness as direct evidence of gene-induced mortality, proved effective and communicable 'wake-up calls' that inbreeding and loss of genetic variation are, or soon could be, a non-trivial constraint on viability of the Scottish chough population. Advanced analyses were therefore highly effective in moving genetics onto conservation practitioners' agendas.

3.5 | Phase five: Integration of ecological and genetic threats

The situation where genetic and ecological constraints interact to determine population viability is likely to be commonplace in small populations, raising challenges for conservation practitioners regarding which is the greater constraint and priority for intervention. Major investment in 'ecological management' (e.g. habitat management to increase natural food) would ultimately be ineffective if λ is, or soon will be, primarily constrained by inbreeding. In the absence of natural immigration, 'genetic management' (e.g. population reinforcement through translocations) would then be required to ameliorate inbreeding, at least until natural landscape connectivity with other populations could be restored. But, such translocations would themselves be ineffective if ecology is currently limiting, and survival and/or reproductive success would be too low to maintain $\lambda \geq 1$ even in an outbred population. Investment in each activity could then be futile without investment in the other.

This situation applies to the chough system, where research phases 1–4 implied that ecological constraints are currently strongly limiting λ, at least partly through food shortage, but that genetic constraints stemming from inbreeding and small N_e could also be limiting. Consequently, we used individual-based models incorporating inbreeding depression alongside environmental and demographic stochasticity to examine the degrees to which ecological management to improve habitat and increase food abundance, and/or genetic management to reduce inbreeding, could increase λ and ultimately population size (Trask et al., 2019). Models were parameterised using spatially structured estimates of baseline vital rates from the long-term demographic monitoring (Reid et al., 2004, 2006), and used the estimated effects of supplementary feeding as a proxy for how much vital rates could potentially be increased through habitat management (Fenn et al., 2020, 2021; Trask et al., 2020). The population-wide degree of inbreeding was estimated from microsatellite variation. However, since there is currently no tractable way to estimate inbreeding load, a plausible range of values was considered, based on wider literature (Trask et al., 2019). Population viability was simulated across scenarios with no conservation management, ecological management only, genetic management only or simultaneous ecological and genetic management.

These simulations showed that, with no management, population extinction is very likely. Ecological management that achieves the same effect as current supplementary feeding was almost sufficient to maintain short-term population stability (Trask et al., 2019). In contrast, translocations on their own were insufficient, because poor environmental conditions meant individuals died regardless of inbreeding. Ecology was therefore identified as the current primary limiting factor, but accumulating inbreeding still caused medium-term population decline (Trask et al., 2019). Simulations that included both ecological and genetic management gave the best outcome, because successful ecological management improved conditions sufficiently for inbreeding depression to be expressed, which was then alleviated by translocations to reduce inbreeding. These simulations highlighted how ecological and genetic constraints can interact. They imply that joint ecological and genetic management will be necessary to achieve the current conservation objective of maintaining a chough population in Scotland, with ecological management as the primary short-term imperative (Trask et al., 2019). The key requirements for successful conservation, at least in terms of chough biology, are now evident (Trask et al., 2020).

4 | DISCUSSION

Investment in population and evolutionary ecology research is often justified by the ambition that resulting advances will ultimately facilitate evidence-based management of populations or species of conservation concern. Yet, the pace of application is often slow (Arlettaz et al., 2010; Cook & Sgrò, 2017; Walsh et al., 2014). Given increasing necessities to reduce biodiversity loss (IPBES, 2019) and to justify research funding, increased efforts at rapid scientific integration and translation are required (Cook et al., 2013; Dubois et al., 2020; Enquist et al., 2017; Haig et al., 2016; Jarvis et al., 2020; Toomey et al., 2016). Our case study summarises our proactive efforts to simultaneously advance population and evolutionary ecology and advance effective conservation of Scottish choughs, and to integrate the two ambitions. Such population-specific reviews have recently been strongly advocated as central to linking fundamental understanding and effective application (Williams et al., 2020), and allow appraisal of which aspects of primary science proved useful, how translation was achieved and what knowledge gaps and constraints on successful conservation remain (e.g. Arlettaz et al., 2010).

4.1 | Research-application integration

During 2001–2021, we completed one major iteration of the desired sequence of (a) rigorous scientific investigation of population ecology, demography and genetics (Reid et al., 2003a, 2003b, 2004, 2006; Trask et al., 2016, 2017) with targeted follow-up investigation of ecological and genetic constraints (Reid et al., 2008, 2009, 2011; Trask et al., 2017; Wenzel et al., 2011, 2012), (b) resulting evidence-based intervention (Bignal & Bignal, 2011; Trask et al., 2020) and (c) rigorous quantitative evaluation of efficacy (Fenn et al., 2020, 2021; Trask et al., 2019). This work is now informing full costing and prioritisation of future chough conservation strategy in Scotland, including decisions on increases or cessation of investment in conservation actions, encompassing future agri-environment schemes and translocations (Trask et al., 2020; Appendix S1). Our case study therefore provides examples of how advanced analyses in population and evolutionary ecology contributed to shaping species-focussed conservation actions, enacted through targeted supplementary feeding, SPA designation and agri-environment schemes. Specifically, the underlying science utilised advanced matrix population model analyses, including prospective analyses of integrated elasticities, retrospective analyses of vital rate variation, approximations of stochastic growth

rates and use of stage-specific reproductive values and demographic variances to estimate N_e (Reid et al., 2004; Trask et al., 2017). It also utilised advanced methodologies for analysing capture–mark–recapture data with random effects, time-varying covariates or multiple states (Fenn et al., 2021; Reid et al., 2003a, 2008), estimation of N_e and relatedness from molecular marker data (Trask et al., 2016, 2017, 2019) and population viability analysis (Trask et al., 2019). We also drew on synthetic knowledge of key parameters that we could not directly estimate, namely the magnitude of inbreeding depression (Trask et al., 2019). All these ingredients directly informed inference on what demographic, ecological and genetic constraints are currently limiting λ, and informed resulting conservation and policy actions.

These conservation-motivated analyses also generated conceptual insights and leading empirical examples that fed back to advance population and evolutionary ecology. For example, efforts to parameterise fully age-structured matrix models, and to understand observed variation in subadult survival, led to new understanding of patterns of age-specific reproductive success, lifelong cohort and spatial effects and parental effects on offspring survival (Reid et al., 2003a, 2003b, 2006, 2010). Efforts to estimate N_e revealed how high demographic variance can drive small N_e/N_c, and identified which sex-age classes contributed most (Trask et al., 2017). Evaluations of interventions showed how compound effects can scale up to determine population outcomes (Fenn et al., 2000, 2021), and how ecology and genetics can interact to shape population viability (Trask et al., 2019). These general conceptual advances would not have been achieved without the underlying ambition of effective conservation application, and associated fieldwork and funding (Appendix S2).

4.2 | Implementation

It is increasingly emphasised that effective conservation science (Figure 1) requires proactive co-working involving diverse researchers, practitioners and wider stakeholders (Arlettaz et al., 2010; Cook et al., 2013; Cook & Sgrò, 2017; Dubois et al., 2020; Enquist et al., 2017; Roux et al., 2019; Taylor et al., 2017; Toomey et al., 2016). Such co-working has been central to our project since 2001. Primary science advances were achieved through direct collaboration between academic researchers with expertise in population and evolutionary ecology and life-history variation (JMR, PM), agricultural ecologists (EB, DIMcC) and Islay farmers with outstanding first-hand knowledge of the focal system and associated land management (EB, SB, leading the SCSG). This team has been embedded within the Scottish Chough Forum, a conservation-focussed group set up in 2001 that also includes representatives from NatureScot and RSPB and additional members of SCSG, with meetings that aim to facilitate joint planning, two-way knowledge transfer, policy discussions and advocacy.

Considerable effort has gone into proactive communication and co-production of knowledge involving scientists, policy-makers, conservation practitioners, farmers, land managers, birdwatchers and the wider interested public, thereby crossing traditional boundaries and actual or perceived value systems (e.g. Cook et al., 2013; Toomey et al., 2016; Williams et al., 2020). To fulfil academic objectives, primary scientific papers were strategically published in British Ecological Society journals, targeted at general concept-led international audiences spanning pure and applied ecology (*Journal of Animal Ecology*: Reid et al., 2003a[†], 2003b[‡], 2004, 2006, 2008, 2010; Trask et al., 2016[†], 2017; *Journal of Applied Ecology*: Reid et al., 2011; Trask et al., 2019; Fenn et al., 2020, 2021; total >685 citations, Google Scholar October 2021, Elton prize [‡]winner, [†]highly commended). Yet, while these papers retained some system-specific context, the focus on general conceptual rather than system-specific impact (as required for these BES journals) meant that the full process of pure–applied integration and its application to chough conservation was not previously visible.

Rather, while the primary papers were important in establishing scientific credibility, key points were communicated to policy-makers through direct conversations and presentations, accessible 'reader's digest' summaries and two substantial reports that contain additional policy-relevant information (Reid et al., 2009; Trask et al., 2020). Major knowledge transfer meetings were held on Islay in 2001, 2008 and 2018, the latter two including discussions with local farmers and land managers. Farmers contributed to undertaking supplementary feeding, observations and providing nest sites, constituting direct participation by the local community. Public presentations were delivered on Islay, and at UK-wide ornithology societies. These activities have been broadly successful in reaching diverse audiences, emphasising the value of plurality in communication and evaluation of scientific outputs (Cook et al., 2013; Roux et al., 2019; Walsh et al., 2014; Williams et al., 2020). Indeed, it is notable that the most cited primary paper (Reid et al., 2003b, 230 citations October 2021) has become an established general reference regarding cross-sectional versus longitudinal variation in age-specific reproductive success, but was least useful in terms of directly informing conservation action. Meanwhile, papers that provide key evidence underpinning the decade-long supplementary feeding intervention are little cited (Reid et al., 2008, 2011; 28 and 19 citations respectively). As shown elsewhere (e.g. Fabian et al., 2019; Walsh et al., 2014), policy-maker attention was most effectively reached through discussions and targeted reports, which are not particularly valued within academic systems.

All research and policy outcomes for the chough system were critically underpinned by the long-term demographic monitoring (i.e. nest recording, colour-ringing and resightings), further illustrating the immense value of such data for both pure and applied purposes. The chough fieldwork objective has been to obtain sufficient data to estimate temporal and spatial variation in key demographic rates, not to attempt close to complete population marking (as is the ambition in some leading field studies in pure population and evolutionary ecology). The chough system has attributes that facilitate such work, notably that all life-history stages are readily observable within Islay's effectively closed population. Yet, 18 years of data

collection (1983–2000) were required even for the initial analyses of vital rate variation (Figure 2). Such long-term fieldwork is often difficult to fund through either pure or applied streams (Clutton-Brock & Sheldon, 2010; Gillson et al., 2019), inhibiting application of cutting-edge concepts and methods in many systems of conservation concern. In our case, monitoring was achieved on a relatively low budget, encompassing substantial intertwined professional and voluntary effort (summarised in Appendix S2).

4.3 | Limitations and prospects

Despite all efforts, the Scottish chough population is still in a perilous state. There were only 43 breeding pairs on Islay in 2018 (and 5 on Colonsay). The recently stable population size on Islay (Figure 2) reflects the ongoing supplementary feeding intervention, which is a positive interim measure but not a long-term solution (Trask et al., 2020). Critical review of the limits of current knowledge and translation is therefore warranted. So far, it has been difficult to incorporate optimal chough management options into the SRDP, or hence facilitate sustainable habitat management. This is partly due to potentially conflicting financial incentives linked to other conservation objectives, and the fact that choughs require complex habitat mosaics that are difficult to provide through simple prescriptive agri-environment measures. There have been insufficient attempts to explicitly link variation in chough demography or invertebrate abundance and availability to agricultural management. Progress here is difficult because data on farm management practices are deemed commercially sensitive and hence not publicly available on small spatial scales, while data on spatio-temporal variation in abundances of diverse invertebrates that choughs of different ages utilise at different times of year have not been systematically collected. Effective year-round monitoring of diverse invertebrate taxa across diverse habitats would be a major challenge, necessitating substantial resources. Any such ambitions cannot be readily achieved through current SRDP programmes, since statutory monitoring of SRDP management focuses on compliance rather than biological impacts, precluding evaluation of efficacy. More targeted farm-specific management agreements and associated biological monitoring in key chough areas may be more effective, and should be considered as the next generations of agri-environment support systems in Scotland are designed. This will in turn require observational, experimental and comparative investigations of effects of agricultural activities such as grazing, silage cutting and livestock treatment regimes, as are now commencing (e.g. MacGillivray et al., 2018; Gilbert et al., 2019; Jonsson et al., 2020; SCSG, unpubl. data). Links between changing agricultural practices, chough foraging ecology and parasite burdens should also be investigated, especially given recent observations of substantial intestinal parasites' burdens in juvenile choughs (Fenn et al., 2021; Trask et al., 2020). Finally, since early analyses suggested the effects of temperature and rainfall on vital rates (Reid et al., 2003a, 2008), potential impacts of climate change should also be projected.

Yet, the science base for conserving the Scottish chough population is already unusually strong. The focal geographical area is relatively small and already subject to extensive management through nature reserves and agri-environment schemes, and there are no major conflicts regarding the broad ambition of conserving choughs. The system therefore represents a test case for successful enaction of evidence-based species-focussed conservation (Figure 1). While policy decisions should of course be taken with appropriate regard for potentially competing societal, economic and ecological priorities, it should be viewed as disappointing if the end point is solely a comprehensive demographic understanding of a population demise.

ACKNOWLEDGEMENTS

The long-term study could not have been achieved without long-term support from numerous people, including Islay farmers and land owners who facilitated access to nest sites and observation locations; all current and previous members of the Scottish Chough Forum; and NatureScot and RSPB (summarised in Appendix S2). We particularly thank Rae McKenzie of NatureScot, without whose enthusiasm and willingness to engage with apparently abstract ideas we would likely never have got beyond phase 1. Aspects of the work were funded by Natural Environment Research Council, NatureScot, University of Aberdeen, University of Glasgow, RSPB, Scottish Government's Strategic Research Programme, Scotland's Rural College, Killam Trusts and the Royal Society (details in Appendix S2). We thank David Jardine for his valuable contributions, and Rae McKenzie, Jess Shaw and Morven Laurie (NatureScot), and Jen Smart, Gillian Gilbert, Jack Fleming and Paul Walton (RSPB) for commenting on a manuscript draft. No specific ethical approval was required for the current paper, which is a review of previously published work.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

J.M.R. drafted the current manuscript. All authors contributed to conceptual development and editing and gave final approval for publication. All authors contributed substantially to data collection, analyses and conceptual developments presented in the primary long-term study papers.

DATA AVAILABILITY STATEMENT

There are no primary data associated with this review manuscript.

ORCID

Jane M. Reid https://orcid.org/0000-0002-5007-7343
Davy I. McCracken https://orcid.org/0000-0001-5057-0448
Amanda E. Trask https://orcid.org/0000-0002-9398-2861

REFERENCES

Allendorf, F. W., Aitken, S. N., Byrne, M., Luikart, G., & Funk, C. (2021). *Conservation and the genomics of populations*. Oxford University Press.

Arlettaz, R., Schaub, M., Fournier, J., Reichlin, T. S., Sierro, A., Watson, J. E. M., & Braunisch, V. (2010). From publications to public actions: When conservation biologists bridge the gap between research and implementation. *BioScience*, *60*, 835–842. https://doi.org/10.1525/bio.2010.60.10.10

Bignal, C., & Bignal, E. (2011). Supplementary feeding of subadult choughs. *British Wildlife*, *22*, 315–319.

Bignal, E., Bignal, S., & McCracken, D. (1997). The social life of the chough. *British Wildlife*, *8*, 373–383.

Bocedi, G., Palmer, S. C. F., Pe'er, G., Heikkinen, R. K., Matsinos, Y. G., Watts, K., & Travis, J. M. J. (2014). RangeShifter: A platform for modelling spatial eco-evolutionary dynamics and species' responses to environmental changes. *Methods in Ecology & Evolution*, *5*, 388–396. https://doi.org/10.1111/2041-210X.12162

Boyce, M. S., Haridas, C. V., Lee, C. T., & NCEAS Stochastic Demography Working Group (2006). Demography in an increasingly variable world. *Trends in Ecology & Evolution*, *21*, 141–148. https://doi.org/10.1016/j.tree.2005.11.018

Bozzuto, C., Biebach, I., Muff, S., Ives, A. R., & Keller, L. F. (2019). Inbreeding reduces long-term growth of Alpine ibex populations. *Nature Ecology & Evolution*, *3*, 1359–1364. https://doi.org/10.1038/s41559-019-0968-1

Caswell, H. (2000). Prospective and retrospective perturbation analyses: Their roles in conservation biology. *Ecology*, *81*, 619–627.

Caswell, H. (2001). *Matrix population models*. Sinauer Associates.

Christie, A. P., Amano, T., Martin, P. A., Shackelford, G. E., Simmons, B. I., & Sutherland, W. J. (2019). Simple study designs in ecology produce inaccurate estimates of biodiversity responses. *Journal of Applied Ecology*, *56*, 2742–2754. https://doi.org/10.1111/1365-2664.13499

Clutton-Brock, T., & Sheldon, B. C. (2010). Individuals and populations: The role of long-term, individual-based studies of animals in ecology and evolutionary biology. *Trends in Ecology & Evolution*, *25*, 562–573. https://doi.org/10.1016/j.tree.2010.08.002

Cook, C. N., Mascia, M. B., Schwartz, M. W., Possingham, H. P., & Fuller, R. A. (2013). Achieving conservation science that bridges the knowledge-action boundary. *Conservation Biology*, *27*, 669–678. https://doi.org/10.1111/cobi.12050

Cook, C. N., & Sgrò, C. N. (2017). Aligning science and policy to achieve evolutionarily enlightened conservation. *Conservation Biology*, *31*, 501–512. https://doi.org/10.1111/cobi.12863

Cooper, E. B., & Kruuk, L. E. B. (2018). Ageing with a silver-spoon: A meta-analysis of the effect of developmental environment on senescence. *Evolution Letters*, *2*, 460–471. https://doi.org/10.1002/evl3.79

Coulson, T., Gaillard, J. M., & Festa-Bianchet, M. (2005). Decomposing the variation in population growth into contributions from multiple demographic rates. *Journal of Animal Ecology*, *74*, 789–801.

Dubois, N. S., Gomez, A., Carlson, S., & Russell, D. (2020). Bridging the research-implementation gap requires engagement from practitioners. *Conservation Science and Practice*, *2*, e134. https://doi.org/10.1111/csp2.134

Eaton, M., Aebischer, N., Brown, A., Hearn, R., Lock, L., Musgrove, A., Noble, D., Stroud, D., & Gregory, R. (2015). Birds of conservation concern 4: The population status of birds in the UK, Channel Islands and Isle of Man. *British Birds*, *108*, 708–746.

Engen, S., Lande, R., & Saether, B. E. (2005). Effective size of a fluctuating age-structured population. *Genetics*, *170*, 941–954. https://doi.org/10.1534/genetics.104.028233

Engen, S., Lande, R., Saether, B. E., & Festa-Bianchet, M. (2007). Using reproductive value to estimate key parameters in density-independent age-structured populations. *Journal of Theoretical Biology*, *244*, 308–317. https://doi.org/10.1016/j.jtbi.2006.08.009

Enquist, C. A. F., Jackson, S. T., Garfin, G. M., Davis, F. W., Gerber, L. R., Littell, J. A., Tank, J. L., Terando, A. J., Wall, T. U., Halpern, B., Hiers, J. K., Morelli, T. L., McNie, E., Stephenson, N. L., Williamson, M. A., Woodhouse, C. A., Yung, L., Brunson, M. W., Hall, K. R., … Shaw, M. R. (2017). Foundations of translational ecology. *Frontiers in Ecology and Environment*, *15*, 541–550. https://doi.org/10.1002/fee.1733

Fabian, Y., Bollmann, K., Brang, P., Heiri, C., Olschewski, R., Rigling, A., Stofer, S., & Holderegger, R. (2019). How to close the science-practice gap in nature conservation? Information sources used by practitioners. *Biological Conservation*, *235*, 93–101. https://doi.org/10.1016/j.biocon.2019.04.011

Fenn, S. R., Bignal, E. M., Bignal, S., Trask, A. E., McCracken, D. I., Monaghan, P., & Reid, J. M. (2021). Within-year and among-year variation in impacts of targeted conservation management on juvenile survival in a threatened population. *Journal of Applied Ecology*. https://doi.org/10.1111/1365-2664.13998

Fenn, S. R., Bignal, E. M., Trask, A. E., McCracken, D. I., Monaghan, P., & Reid, J. M. (2020). Collateral benefits of targeted supplementary feeding on demography and growth rate of a threatened population. *Journal of Applied Ecology*, *57*, 2212–2221. https://doi.org/10.1111/1365-2664.13721

Frankham, R., Ballou, J. D., Ralls, K., Eldridge, M. D. B., Dudash, M. R., Fenster, C. B., Lacy, R. C., & Sunnucks, P. (2017). *Genetic management of fragmented animal and plant populations*. Oxford University Press.

Frankham, R., Bradshaw, C. J. A., & Brook, B. W. (2014). Genetics in conservation management: Revised recommendations for the 50/500 rules, Red List criteria and population viability analyses. *Biological Conservation*, *170*, 56–63. https://doi.org/10.1016/j.biocon.2013.12.036

Gaillard, J. M., Festa-Bianchet, M., & Yoccoz, N. G. (1998). Population dynamics of large herbivores: Variable recruitment with constant adult survival. *Trends in Ecology & Evolution*, *13*, 58–63. https://doi.org/10.1016/S0169-5347(97)01237-8

Gilbert, G., MacGillivray, F. S., Robertson, H. L., & Jonsson, N. N. (2019). Adverse effects of routine bovine health treatments containing triclabendazole and synthetic pyrethroids on the abundance of dipteran larvae in bovine faeces. *Scientific Reports*, *9*, 4315. https://doi.org/10.1038/s41598-019-40800-6

Gillson, L., Biggs, H., Smit, I. P. J., Virah-Sawmy, M., & Rogers, K. (2019). Finding common ground between adaptive management and evidence-based approaches to biodiversity conservation. *Trends in Ecology & Evolution*, *34*, 31–44. https://doi.org/10.1016/j.tree.2018.10.003

Gimenez, O., Viallefont, A., Charmantier, A., Pradel, R., Cam, E., Brown, C. R., Anderson, M. D., Brown, M. B., Covas, R., & Gaillard, J. M. (2008). The risk of flawed inference in evolutionary studies when detectability is less than one. *The American Naturalist*, *172*, 441–448. https://doi.org/10.1086/589520

Green, R. (2020). Corncrake conservation. *British Birds*, *113*, 671–685.

Haig, S. M., Miller, M. P., Bellinger, R., Draheim, H. M., Mercer, D. M., & Mullins, T. D. (2016). The conservation genetics juggling act: Integrating genetics and ecology, science and policy. *Evolutionary Applications*, *9*, 181–195. https://doi.org/10.1111/eva.12337

Hayhow, D. B., Johnstone, I., Moore, A. S., Mucklow, C., Stratford, A., Šúr, M., & Eaton, M. A. (2018). Breeding status of red-billed choughs *Pyrrhocorax pyrrhocorax* in the UK and Isle of Man in 2014. *Bird Study*, *65*, 458–470.

Hilde, C. H., Gamelon, M., Sæther, B. E., Gaillard, J. M., Yoccoz, N. G., & Pélabon, C. (2020). The demographic buffering hypothesis: Evidence and challenges. *Trends in Ecology & Evolution*, *35*, 523–538. https://doi.org/10.1016/j.tree.2020.02.004

Hoffmann, M., Hilton-Taylor, C., Angulo, A., Böhm, M., Brooks, T. M., Butchart, S. H. M., Carpenter, K. E., Chanson, J., Collen, B., Cox, N. A., Darwall, W. R. T., Dulvy, N. K., Harrison, L. R., Katariya, V., Pollock, C. M., Quader, S., Richman, N. I., Rodrigues, A. S. L., Tognelli, M. F., … Stuart, S. N. (2010). The impact of conservation

on the status of the world's vertebrates. *Science*, *330*, 1503–1509. https://doi.org/10.1126/science.1194442

IPBES. (2019). *Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services* (S. Díaz, J. Settele, E. S. Brondízio, H. T. Ngo, M. Guèze, J. Agard, A. Arneth, P. Balvanera, K. A. Brauman, S. H. M. Butchart, K. M. A. Chan, L. A. Garibaldi, K. Ichii, J. Liu, S. M. Subramanian, G. F. Midgley, P. Miloslavich, Z. Molnár, D. Obura, A. Pfaff, S. Polasky, A. Purvis, J. Razzaque, B. Reyers, R. Roy Chowdhury, Y. J. Shin, I. J. Visseren-Hamakers, K. J. Willis, & C. N. Zayas [Eds.], p. 56). IPBES secretariat. https://doi.org/10.5281/zenodo.3553579

Jarvis, R. M., Borrelle, S. B., Forsdick, N. J., Pérez-Hämmerle, K.-V., Dubois, N. S., Griffin, S. R., Recalde-Salas, A., Buschke, F., Rose, D. C., Archibald, C. L., Gallo, J. A., Mair, L., Kadykalo, A. N., Shanahan, D., & Prohaska, B. K. (2020). Navigating spaces between conservation research and practice: Are we making progress? *Ecological Solutions and Evidence*, *1*, e12028. https://doi.org/10.1002/2688-8319.12028

Jonsson, N. N., Gilbert, G., & MacGillivray, F. S. (2020). Livestock management in red-billed chough feeding habitat in Great Britain and the Isle of Man. *Rangeland Ecology & Management*, *73*, 2016–2223. https://doi.org/10.1016/j.rama.2019.10.009

Lacy, R. C., & Pollak, J. P. (2017). *Vortex: A stochastic simulation of the extinction process*. Chicago Zoological Society.

Laiolo, P., Bignal, E. M., & Patterson, I. J. (1998). The dynamics of parental care in choughs (*Pyrrhocorax pyrrhocorax*). *Journal für Ornithologie*, *139*, 297–305. https://doi.org/10.1007/BF01653340

Lindström, J. (1999). Early development and fitness in birds and mammals. *Trends in Ecology & Evolution*, *14*, 343–348. https://doi.org/10.1016/S0169-5347(99)01639-0

MacGillivray, F. S., Gilbert, G., & McKay, C. R. (2018). The diet of a declining red-billed chough *Pyrrhocorax pyrrhocorax* population on Islay, Scotland. *Bird Study*, *65*, 422–425.

Maness, T. J., & Anderson, D. J. (2013). Predictors of juvenile survival in birds. *Ornithological Monographs*, *78*, 1–55. https://doi.org/10.1525/om.2013.78.1.1

McCracken, D. I., & Foster, G. N. (1994). Invertebrates, cow dung and the availability of potential food for the chough, *Pyrrhocorax pyrrhocorax* L., on pastures in north-west Islay. *Environmental Conservation*, *21*, 262–266.

McCracken, D. I., Foster, G. N., Bignal, E. M., & Bignal, S. (1992). An assessment of chough, *Pyrrhocorax pyrrhocorax*, diet using multivariate analysis methods. *Avocetta*, *16*, 19–29.

Nichols, J. D., & Kendall, W. L. (1995). The use of multi-state capture-recapture models to address questions in evolutionary ecology. *Journal of Applied Statistics*, *22*, 835–846. https://doi.org/10.1080/02664769524658

Pigeon, G., Loe, L. E., Bischof, R., Bonenfant, C., Forchhammer, M., Irvine, R. J., Ropstad, E., Stien, A., Veiberg, V., & Albon, S. (2019). Silver spoon effects are constrained under extreme adult environmental conditions. *Ecology*, *100*, e02886. https://doi.org/10.1002/ecy.2886

Reid, J. M., Bignal, E. M., Bignal, S., Bogdanova, M. I., Monaghan, P., & McCracken, D. I. (2011). Diagnosing the timing of demographic bottlenecks: Sub-adult survival in red-billed choughs. *Journal of Applied Ecology*, *48*, 797–805. https://doi.org/10.1111/j.1365-2664.2011.01973.x

Reid, J. M., Bignal, E. M., Bignal, S., McCracken, D. I., Bogdanova, M. I., & Monaghan, P. (2008). Investigating patterns and processes of demographic variation: Environmental correlates of pre-breeding survival in red-billed choughs *Pyrrhocorax pyrrhocorax*. *Journal of Animal Ecology*, *77*, 777–788. https://doi.org/10.1111/j.1365-2656.2008.01400.x

Reid, J. M., Bignal, E. M., Bignal, S., McCracken, D. I., & Monaghan, P. (2003a). Environmental variability, life-history covariation and cohort effects in the red-billed chough *Pyrrhocorax pyrrhocorax*. *Journal of Animal Ecology*, *72*, 36–46. https://doi.org/10.1046/j.1365-2656.2003.00673.x

Reid, J. M., Bignal, E. M., Bignal, S., McCracken, D. I., & Monaghan, P. (2003b). Age-specific reproductive performance in red-billed choughs *Pyrrhocorax pyrrhocorax*: Patterns and processes in a natural population. *Journal of Animal Ecology*, *72*, 765–776. https://doi.org/10.1046/j.1365-2656.2003.00750.x

Reid, J. M., Bignal, E. M., Bignal, S., McCracken, D. I., & Monaghan, P. (2004). Identifying the demographic determinants of population growth rate: A case study of red-billed choughs *Pyrrhocorax pyrrhocorax*. *Journal of Animal Ecology*, *73*, 777–788. https://doi.org/10.1111/j.0021-8790.2004.00854.x

Reid, J. M., Bignal, E. M., Bignal, S., McCracken, D. I., & Monaghan, P. (2006). Spatial variation in demography and population growth rate: The importance of natal location. *Journal of Animal Ecology*, *75*, 1201–1211. https://doi.org/10.1111/j.1365-2656.2006.01143.x

Reid, J. M., Bignal, E., Bignal, S., McCracken, D. I., & Monaghan, P. (2010). Parent age, lifespan and offspring survival: Structured variation in life-history in a wild population. *Journal of Animal Ecology*, *79*, 851–862. https://doi.org/10.1111/j.1365-2656.2010.01669.x

Reid, J. M., Bogdanova, M., Bignal, E., Bignal, S., McCracken, D. I., & Monaghan, P. (2009). Population ecology and conservation of red-billed choughs. Research and Policy Report to Scottish Natural Heritage & Royal Society for Protection of Birds. Retrieved from http://nora.nerc.ac.uk/id/eprint/517111/

Roux, D. J., Kingsford, R. T., Cook, C. N., Carruthers, J., Dickson, K., & Hockings, M. (2019). The case for embedding researchers in conservation agencies. *Conservation Biology*, *33*, 1266–1274. https://doi.org/10.1111/cobi.13324

Salguero-Gómez, R., Jones, O. R., Archer, C. R., Bein, C., de Buhr, H., Farack, C., Gottschalk, F., Hartmann, A., Henning, A., Hoppe, G., Römer, G., Ruoff, T., Sommer, V., Wille, J., Voigt, J., Zeh, S., Vieregg, D., Buckley, Y. M., Che-Castaldo, J., … Vaupel, J. W. (2016). COMADRE: A global data base of animal demography. *Journal of Animal Ecology*, *85*, 371–384. https://doi.org/10.1111/1365-2656.12482

Stanbury, A., Brown, A., Eaton, M., Aebischer, N., Gillings, S., Hearn, R., Noble, D., Stroud, D., & Gregory, R. (2017). The risk of extinction for birds in Great Britain. *British Birds*, *110*, 502–517.

Still, E., Monaghan, P., & Bignal, E. (1987). Social structuring at a communal roost of choughs *Pyrrhocorax pyrrhocorax*. *Ibis*, *129*, 398–403. https://doi.org/10.1111/j.1474-919X.1987.tb03186.x

Taylor, H. R., Dussex, N., & van Heezik, Y. (2017). Bridging the conservation genetics gap by identifying barriers to implementation for conservation practitioners. *Global Ecology and Conservation*, *10*, 231–242. https://doi.org/10.1016/j.gecco.2017.04.001

Toomey, A. H., Knight, A. T., & Barlow, J. (2016). Navigating the space between research and implementation in conservation. *Conservation Letters*, *10*, 619–625. https://doi.org/10.1111/conl.12315

Trask, A. E., Bignal, E., Bignal, S., McCracken, D. I., Fenn, S. R., Monaghan, P., & Reid, J. M. (2020). Conservation strategy for red-billed choughs in Scotland: Assessment of the impact of supplementary feeding and evaluation of future management strategies. Commissioned Research Report for NatureScot.

Trask, A. E., Bignal, E. M., McCracken, D. I., Monaghan, P., Piertney, S. B., & Reid, J. M. (2016). Evidence of the phenotypic expression of a lethal recessive allele under inbreeding in a wild population of conservation concern. *Journal of Animal Ecology*, *85*, 879–891. https://doi.org/10.1111/1365-2656.12503

Trask, A. E., Bignal, E., McCracken, D. I., Piertney, S. B., & Reid, J. M. (2017). Estimating demographic contributions to effective population size in an age-structured wild population experiencing environmental

and demographic stochasticity. *Journal of Animal Ecology*, *86*, 1082–1093. https://doi.org/10.1111/1365-2656.12703

Trask, A. E., Fenn, S., Bignal, E., McCracken, D. I., Monaghan, P., & Reid, J. M. (2019). Evaluating the efficacy of independent versus simultaneous management strategies to address ecological and genetic threats to population viability. *Journal of Applied Ecology*, *56*, 2264–2273. https://doi.org/10.1111/1365-2664.13464

van de Pol, M., Bruinzeel, L. W., Heg, D., van der Jeugd, H. P., & Verhulst, S. (2006). A silver spoon for a golden future: Long-term effects of natal origin on fitness prospects of oystercatchers (*Haematopus ostralegus*). *Journal of Animal Ecology*, *75*, 616–626. https://doi.org/10.1111/j.1365-2656.2006.01079.x

van Tienderen, P. H. (1995). Life cycle trade-offs in matrix models. *Ecology*, *76*, 2482–2489.

Walsh, J. C., Dicks, L. V., & Sutherland, W. J. (2014). The effect of scientific evidence on conservation practitioners' management decisions. *Conservation Biology*, *29*, 88–98. https://doi.org/10.1111/cobi.12370

Wenzel, M. A., Webster, L. M. I., Blanco, G., Burgess, M. D., Kerbiriou, C., Segelbacher, G., Piertney, S. B., & Reid, J. M. (2012). Pronounced genetic structure and low genetic diversity in European red-billed chough (*Pyrrhocorax pyrrhocorax*) populations. *Conservation Genetics*, *13*, 1213–1230. https://doi.org/10.1007/s10592-012-0366-6

Wenzel, M. A., Webster, L. M. I., Segelbacher, G., Reid, J. M., & Piertney, S. B. (2011). Isolation and characterisation of 17 microsatellite loci for the red-billed chough (*Pyrrhocorax pyrrhocorax*). *Conservation Genetics Resources*, *3*, 737–740. https://doi.org/10.1007/s12686-011-9446-z

White, G. C., & Burnham, K. P. (1999). Program MARK: Survival estimation from populations of marked animals. *Bird Study*, *46*, 120–139. https://doi.org/10.1080/00063659909477239

Williams, D. R., Balmford, A., & Wilcove, D. S. (2020). The past and future role of conservation science in saving biodiversity. *Conservation Letters*, *13*, e12720. https://doi.org/10.1111/conl.12720

Wisdom, M. J., Mills, L. S., & Doak, D. F. (2000). Life stage simulation analysis: Estimating vital-rate effects on population growth for conservation. *Ecology*, *81*, 628–641.

Wotton, S. R., Eaton, M., Ewing, S. R., & Green, R. E. (2015). The increase in the Corncrake *Crex crex* population of the United Kingdom has slowed. *Bird Study*, *62*, 486–497.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Reid, J. M., Bignal, E., Bignal, S., McCracken, D. I., Fenn, S. R., Trask, A. E., & Monaghan, P. (2022). Integrating advances in population and evolutionary ecology with conservation strategy through long-term studies of red-billed choughs. *Journal of Animal Ecology*, 91, 20–34. https://doi.org/10.1111/1365-2656.13615